

Factors controlling the frequency and biomass of submerged vegetation in outwash lakes supplied with surface water or groundwater

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We analysed the frequency and biomass of submerged plants in 1490 samples taken from 10 lakes located in the same geological formation (outwash) and fed with surface water (1st lake group, $n = 540$ samples) or groundwater (2nd group, $n = 950$). In the first group, mosses were very frequent (mean \pm SD = $90.0\% \pm 18.2\%$), while acidophilous vascular plants were less frequent ($23.9\% \pm 32.5\%$) and their biomass was low. There was one dominant species: *Sphagnum denticulatum*. In the second group, calciphilous vascular plants and stoneworts were in the majority, with relatively higher frequencies ($40.1\% \pm 25.2\%$ and $59.7\% \pm 23.2\%$) and biomass (5.1 ± 6.5 and 13.8 ± 20.5 g DW 0.1 m^{-2}). In the lakes fed with surface water, water pH was the factor controlling the frequency of mosses and vascular plants. In the group of lakes supplied with groundwater, sediment conductivity and calcium governed the frequency of stoneworts. Moss biomass depended on conductivity, total phosphorus and calcium concentrations in the water, while stonewort biomass depended on sediment conductivity. For both types of water supply, submerged plant frequency and biomass in the lakes were controlled more strongly by non-nutrient than by nutrient factors.

Introduction

Plant communities in lakes are formed in the context of specific climatic, geological and limnological conditions; the flora of lakes develops under the influence of water and sediment properties (Barko and James 1998, Kłosowski 2006), irradiance (Schwarz *et al.* 2000, Schwarz *et al.* 2002) and competition, both interspecific (Lodge *et al.* 1998, Chmara *et al.* 2013) and intrapopulational (Szmeja *et al.* 2010). In some circumstances, wave activity, vertical water fluctuations (Szmeja 1994a,

Madsen *et al.* 2001) and human pressure (Mitchell and Perrow 1998) may also become important.

In northwestern Poland, about 100 km south of the Baltic Sea, exists a large outwash formation with radically different lakes: soft waters and hard waters. The former are dominated by isoetids and acidic mosses (Szmeja 2010, Szmeja *et al.* 2010), the latter by neutral vascular plants and charophytes (Chmara and Bociąg 2007, Bociąg and Chmara 2008). The causes for such differences in lakes located right next to each other are not fully known.

The outwash formation is formed by acid sand and gravel. However, there is often a layer rich in calcium carbonate or dispersed inclusions of calcium, known as the “rock flower” (Kachnic and Kachnic 2006). If the lake basin crosses the layer or is supplied with groundwater, then the lake is alkaline or neutral; otherwise it is acidic due to surface water flowing down the slopes of the basin. The way water is supplied can affect the type of vegetation in a lake.

The structure of vegetation in lakes depends on physical and chemical environmental factors, e.g., on water pH and concentration of carbon for photosynthesis (Madsen and Sand-Jensen 1991, Riis and Sand-Jensen 1998, Vestergaard and Sand-Jensen 2000). The frequency and biomass of macrophytes is apparent from the species composition, species turnover within lakes and among them, as well as the nestedness of species in the depth zones (Chmara *et al.* 2013).

For this study we selected small forest lakes (1) fed from a known (hydrologically proven) source, (2) located in the same geological formation, and (3) whose catchment slopes are covered with the same vegetation, without signs of human pressure. Each lake is situated in an outwash formation and supplied with surface water (from precipitation or slopes) or groundwater (Bajkiewicz-Grabowska 2006). The former group receives nutrient-poor precipitation water which earlier rinsed the acidic undergrowth of a pine forest and the surface layer of sand, whereas the latter receives alkaline groundwater rich in calcium. Therefore, the aim of this study is to determine which environmental factors control frequency, biomass and species composition in lakes situated in a subboreal outwash formation.

Material and methods

Study area

The studies were conducted on the Charzykowy Plain, situated on a vast outwash plain from the Pleistocene glaciation in NW Poland (Fig. 1). The lakes are located in the Pomeranian Lakeland along the southern shores of the Baltic Sea, in a cold temperate climate. *Pinus sylvestris* forest is dominant there, with numerous lakes,

peatlands and small rivers. Almost the entire area is within the Tuchola Pine Forest National Park (53°47'N, 17°35'E, biosphere reserve, MAB programme) and Zaborski Landscape Park (53°48'N, 17°36'E). Human pressure on the lakes there is limited.

The lakes of the Charzykowy Plain vary in surface area (2.5–280.7 ha), maximum depth (4.5–43.0 m) and mean depth (2.0–10.7 m; Table 1). On the Charzykowy Plain the lake basins are entirely or partially depressed in the outwash plain. Their basin slope surfaces are covered with eolian, acidic and barren sand. Under this layer are sedimentary deposits which are more varied geologically and chemically, and glaciofluvials containing rock flour rich in calcium carbonate (Bukowska-Jania 2003). The catchment areas of the lakes are almost entirely covered by pine forests. The selected lakes exhibit gradients from acid to alkaline and from shallow to fairly deep (cf. Tables 1 and 2).

The majority of small outwash lakes without flow-through are supplied with surface water (precipitation infiltrating the pine forest undergrowth, soil and upper layer of the outwash plain) or water from the underground hydrological system. According to Bajkiewicz-Grabowska (2006), the lakes in the study area fed with surface water are Kocioł, Moczadło, Małe Łowne, Czarne and Sierzywk, and the ones supplied with groundwater are Ostrowite, Gardliczno Wielkie, Nawionek, Zmarłe and Borzyszkowskie (Table 1). The first group receives acidic, nutrient-poor water, and the latter group receives alkaline water richer in dissolved salts, especially salts of calcium. We studied the processes by which aquatic plants form assemblages in these lakes.

Sampling design

In each of the ten lakes we demarcated two transects of lake bottom, each 150 m wide, perpendicular to the lake shore and running from the shallow littoral zone to the bottom (deep) limit of plant occurrence. These transects were divided into depth zones every 1.0 m. We collected plant, water and sediment samples from them. In total, we collected 1490 plant samples, each cover-



Fig. 1. Location of the study area in NW Poland (top) and locations of the studied lakes (1–10) on the Charzykowy Plain (bottom). Lakes: 1 = Czarne, 2 = Moczadło, 3 = Sierzywk, 4 = Małe Łowne, 5 = Kocioł, 6 = Ostrowite, 7 = Borzyszkowskie, 8 = Gardliczno Duże, 9 = Zmarłe 10 = Nawionek.

ing 0.1 m², from these 20 bottom transects: 540 from lakes fed with surface water, and 950 from those supplied with groundwater. A diver collected plant samples, according to Madsen and Adams (1988), Madsen (1993) and Banaś *et al.* 2012. On the day of collection the samples were transported to the laboratory, where the plants were segregated into species and dried to constant weight and weighed to the nearest 0.01 g. The material was collected during the vegetation seasons (in June and August) of the years 2004–2006.

The physical and chemical properties of the lake sediments within the transects were deter-

Table 1. Characteristics of lakes supplied with surface water (1–5) and groundwater (6–10).

No. and name	Area (ha)	Max.–min. depth (m)	Maximum depth (m) of plant occurrence
1. Czarne	8.7	7.8–4.0	7
2. Moczadło	3.6	12.0–6.5	10
3. Sierzywk	3.5	4.5–2.0	2
4. Małe Łowne	2.9	7.0–3.5	3
5. Kocioł	2.5	11.0–7.2	10
6. Ostrowite	280.7	43.0–10.7	10
7. Borzyszkowskie	101.2	31.0–7.7	5
8. Gardliczno	44.5	26.5–7.5	10
9. Zmarłe	29.6	19.4–9.3	10
10. Nawionek	10.2	10.0–6.5	9

mined on the basis of three samples of the upper sediment layer (5–10 cm) and three samples of above-sediment water (5–10 cm above the bottom) collected from the depth zones every 1.0 m. In total, 447 sediment samples and the same number of above-sediment water samples were taken. The following were measured from the sediment: pH, conductivity ($\mu\text{S cm}^{-1}$), hydration (%) and content of organic matter (OM, %), calcium ($\text{mg Ca g}^{-1} \text{ DW}$ = dry weight), total phosphorus (P_{tot} $\text{mg g}^{-1} \text{ DW}$) and silica (SiO_2 , %). From the water, the following were determined: pH, conductivity ($\mu\text{S cm}^{-1}$), total hardness (mg CaO l^{-1}), and content of calcium (mg l^{-1}), total nitrogen (N_{tot} mg l^{-1}) and total phosphorus (P_{tot} mg l^{-1}). The measurements were performed using methods suggested by Eaton *et al.* (2005).

Data analysis

The frequency of species was calculated from the quotient of its occurrence in the samples. The relationship between the frequency and biomass of plants and environmental factors was determined using multiple regression and canonical analyses (ter Braak 1987, Gittins 1985). We considered non-nutrient water variables (NNVW: pH, conductivity, total hardness, calcium con-

centration) and non-nutrient sediment variables (NNVS: pH, conductivity, calcium concentration), as well as nutrient water variables (NVW: concentrations of P_{tot} and N_{tot}) and nutrient sediment variables (NVS: P_{tot} , organic matter). The relationship of the frequency and biomass of 29 species to the nutrient and non-nutrient variables was determined by canonical analysis incorporating sediment and sediment water properties.

The data for the analyses were standardized in CANOCO 4.5 (ter Braak and Šmilauer 2002). Detrended correspondence analysis (DCA) showed that all the data on plant biomass and frequency and water and sediment properties were linear in structure and represented only part of a Gaussian distribution (eigenvalues < 2 SD), thereby calling for the use of redundancy (RDA) analyses (ter Braak and Šmilauer 2002). By using redundancy analysis (RDA; ter Braak 1986, 1987, 1988) we determined the ordering of the frequency and biomass of aquatic plants in terms of the physicochemical properties of sediment water and sediment. Statistical significance of the environmental parameters was tested using the Monte Carlo permutation test with 999 permutations.

We analysed the variation of the lakes' aquatic environments by non-metric multidimensional scaling (NMDS; Kruskal 1964, Clarke

Table 2. Properties (mean \pm SD, DW = dry weight) of water and sediment in lakes supplied with surface water (S) and groundwater (G). Significant differences between lake groups (G, S) are indicated with asterisks (* $p < 0.05$, ** $p < 0.001$), n.s. = not significant.

	Mean \pm SD		Median		Min.–Max.	
	S	G	S	G	S	G
Water						
pH	5.3 \pm 0.8**	8.1 \pm 0.4**	5.5	8.25	3.8–6.7	6.7–8.7
Conductivity ($\mu\text{S cm}^{-1}$)	29.9 \pm 5.8**	177.0 \pm 59.5**	27.0	182	23.2–41.4	52–274
Total hardness (mg l^{-1})	3.4 \pm 0.7**	48.5 \pm 17.1**	3.1	42.8	2.4–5.3	19.4–85.6
Ca^{2+} (mg l^{-1})	1.7 \pm 0.9**	29.6 \pm 11.8**	1.5	31.4	0.6–3.7	5.2–46.7
N_{tot} (mg l^{-1})	1.4 \pm 0.4 n.s.	0.86 \pm 0.5 n.s.	1.3	0.68	0.5–2.3	0.04–2.83
P_{tot} (mg CaO l^{-1})	0.02 \pm 0.03**	0.07 \pm 0.03**	0.008	0.06	0.0005–0.09	0.05–0.28
Sediment						
pH	5.8 \pm 0.5**	7.2 \pm 0.4**	5.82	7.28	4.7–6.9	6.2–7.8
Conductivity ($\mu\text{S cm}^{-1}$)	27.1 \pm 19.1**	219.1 \pm 112.9**	24.0	233.5	8.0–114.0	58.0–592.0
Hydration (%)	54.1 \pm 29.1 n.s.	61.9 \pm 24.3 n.s.	42.0	68.3	19.5–92.2	10.0–93.5
Organic matter (%)	2.0 \pm 1.9**	17.5 \pm 22.7**	1.4	8.6	0.1–6.8	0.5–80.2
Ca^{2+} ($\text{mg g}^{-1} \text{ DW}$)	3.1 \pm 2.0**	67.6 \pm 103.2**	2.6	9.8	1.1–9.3	1.1–392.3
P_{tot} ($\text{mg g}^{-1} \text{ DW}$)	1.8 \pm 2.3**	0.44 \pm 0.42**	0.4	0.37	0.03–7.4	0.001–1.8
SiO_2 (%)	87.1 \pm 2.4*	63.3 \pm 34.3*	97.9	81.6	70.1–99.5	0.1–99.1

1993), which creates an ordination plot from a matrix of similarities among samples, here a matrix of Bray-Curtis similarities (Bray and Curtis 1957). The NMDS algorithm was then used to construct a plot in which rank similarities were preserved as Bray-Curtis distances between samples. The NMDS analysis used PAST ver. 2.03 (Hammer et al. 2001).

Results

Environmental conditions

The water in the lakes supplied with surface flow was acidic (pH mean \pm SD = 5.3 ± 0.8 ; Me = 5.5) and poor in calcium (1.7 ± 0.9 mg l⁻¹; Table 2). The sediment was acidic, well hydrated and low in organic matter content, had low conductivity, contained little calcium and phosphorus, and had a very high silica content ($87.1\% \pm 2.4\%$; Table 2).

The water in the lakes fed from underground sources had a pH ranging from neutral to alkaline (6.7–8.7) and high conductivity. The water was hard, containing a high amount of calcium (29.6 ± 11.8 mg l⁻¹) and moderate concentrations of P_{tot} (0.07 ± 0.03 mg l⁻¹) and N_{tot} (0.86 ± 0.5 mg l⁻¹). Siliceous and carbonate mineral substances, including silica (SiO₂) representing $63.3\% \pm 34.3\%$, were the main components of the sediment. Its pH varied from slightly acidic to alkaline (6.2–7.8). It was well hydrated and characterized by high conductivity, and contained much calcium and little phosphorus.

The NMDS analysis results for the six selected water characteristics and seven sediment properties (see Material and methods) showed that the limnic environments varied according to the source of water supply. The first axis explained 93.7% of the variation and was strongly correlated with calcium concentration ($r = 0.95$), conductivity ($r = 0.95$), total hardness ($r = 0.90$) and pH ($r = 0.82$; Fig. 2). The physical and chemical properties of sediment varied slightly less (the first axis explained 79.2% of the variation, Fig. 2). As in the case of water, conductivity ($r = 0.81$), pH ($r = 0.74$) and calcium content ($r = 0.65$) of sediments were the properties most correlated with the first axis.

Vegetation structure

Vegetation structure was determined on the basis of the number of species and their frequency and biomass. Eight submerged plant species were found in the lakes fed with surface water. The mean number of species per sample ($n = 540$, each covering 0.1 m²) was 1.33 ± 0.7 (skewness = 2.17), and 75% of the samples contained one species. Mosses (mainly *Sphagnum denticulatum*) had the highest frequency (67.7%). Vascular plants, predominantly isoetids such as *Isoetes lacustris* (26.5%) and *Lobelia dortmanna* (11.3%), were less frequent. Stoneworts, for example *Nitella syncarpa* (1.5%), occurred sporadically (Table 3). The bryophyte *Sphagnum denticulatum* represented 71.8% of the total biomass of submerged vegetation.

In the lakes supplied with groundwater, 25 submerged plant species were recorded. The mean number of species per sample ($n = 950$) was 1.67 ± 0.8 (skewness = 1.47). The littoral zone was most often occupied by stoneworts and vascular plants, rarely mosses: *Nitella flexilis*, *Myriophyllum spicatum*, *Potamogeton pectinatus*, *Chara tomentosa* and *C. delicatula* were most frequent (Table 3). In terms of shares of total biomass there were several subdominants, mainly stoneworts (*Chara tomentosa*, *Nitella flexilis*, *C. delicatula*) instead of one dominant species. These species represented more than half (52.2%) of total plant biomass in this lake category.

The vegetation structure in the outwash lakes varied according to the source of water supply. By frequency, the ordering of species groups in the lakes fed with surface water was mosses > vascular plants > stoneworts; in the lakes supplied with groundwater the ordering was stoneworts > vascular plants > mosses. The former had a dominant species, and the latter did not.

Factors controlling species frequency

In the lakes supplied with surface flow, the frequencies of bryophytes, vascular plants and stoneworts were high, lower and the lowest, respectively (Table 4). Redundancy analysis indicated that the high frequency of bryophytes depended on low water and sediment pH in

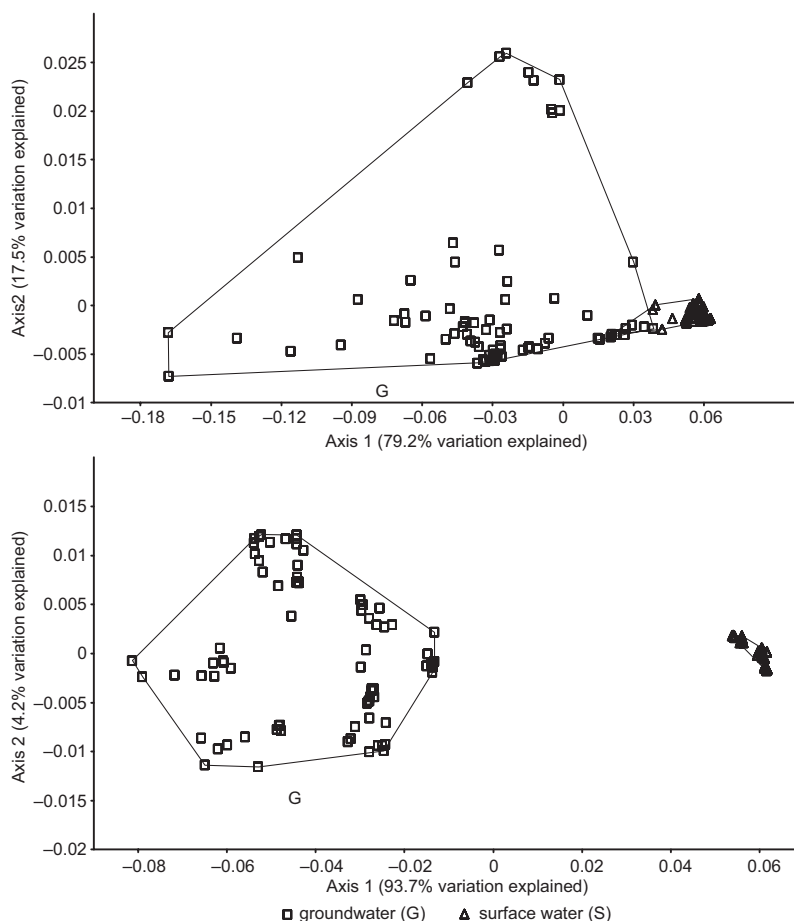


Fig. 2. Sources of supply to the studied lakes, and properties of water (upper diagram) and sediment (lower diagram). G = groundwater; S = surface water. The analysis took into account 6 properties of water and 7 properties sediment (see Table 2).

the lakes fed with surface water (Fig. 3). Water properties governed the frequency of bryophyte occurrence: in multiple regression analysis, those factors explained 61.0% of the variation ($r^2 = 0.61$, $p < 0.001$), while sediment characteristics explained less than 40.0%. The frequency of bryophytes in acidic and non-carbonate water was high, reaching $90.0\% \pm 18.2\%$. When water pH in such lakes exceeded 6.0, the frequency of bryophytes fell by half to $40.0\% \pm 35.7\%$ ($p < 0.001$). *Sphagnum denticulatum*, which was the dominant species in the submerged vegetation, was the most common bryophyte. The frequency of vascular plants, particularly isoetids, was lower ($23.9\% \pm 32.5\%$) and was positively correlated with water and sediment pH, and to a lesser extent also with sediment hydration (Fig. 3 upper diagram).

In the lakes supplied with groundwater, the frequency of stoneworts was the highest

frequency, while that of vascular plants was slightly lower (Table 4). The frequency of vascular plants was related to the phosphorus content of the sediment. Stoneworts occurred at very high frequency in the littoral zones, and this was dependent on the calcium, hydration of the sediment and conductivity. We verified this RDA-based finding by subjecting the data to multiple regression (Fig. 3). The outcome was that the frequency of stoneworts in the groundwater-fed lakes was controlled by sediment properties, not by sediment water properties, the effect of which was not significant ($r^2 < 0.1$, $p > 0.05$). Multiple regression analysis confirmed this. The frequency of stoneworts depended mainly on sediment conductivity: when conductivity was $< 135 \mu\text{S cm}^{-1}$, the frequency was $49.6\% \pm 38.8\%$, but when conductivity was $> 255 \mu\text{S cm}^{-1}$, the frequency was $78.3\% \pm 31.3\%$ ($p < 0.01$). Stoneworts such as *Nitellopsis obtusa*, *Chara*

tomentosa and *C. rudis* were very frequent when conductivity values were high.

A comparison of the factors controlling plant frequency indicated that in the surface-fed lakes the frequency of bryophytes was negatively correlated with most of the environmental factors, while the frequency of vascular plants was positively correlated with them.

Factors controlling species biomass

The mean bryophyte biomass in lakes fed with surface water was relatively high (mean \pm SD = 9.6 ± 6.2 g DW 0.1 m^{-2}), and ranged from 0.1 to $45.6 \text{ g DW } 0.1 \text{ m}^{-2}$ in the samples. Bryophytes occurred throughout the littoral zone at 0.1–10.0 m depth. The share of *Sphagnum denticulatum* in total plant biomass was the highest (72.5%). Bryophyte biomass depended on water properties, mainly conductivity and the content of calcium and P_{tot} ($r^2 = 0.40$, $p < 0.0001$; RDA 40%). Vascular plant biomass was positively correlated with water hardness and sediment pH and did not differ from the biomass of bryophytes (8.9 ± 6.8 g DW 0.1 m^{-2} vs. 9.6 ± 6.2 g DW 0.1 m^{-2} ; $p > 0.05$). In groundwater-fed lakes, bryophytes were represented by two species, *Fontinalis antipyretica* and *Drepanocladus aduncus*, which had low frequencies and biomass (Table 4). Factors controlling the biomass of this group are not analysed here any further.

The mean biomass of vascular plants was higher than that of bryophytes. We found a sta-

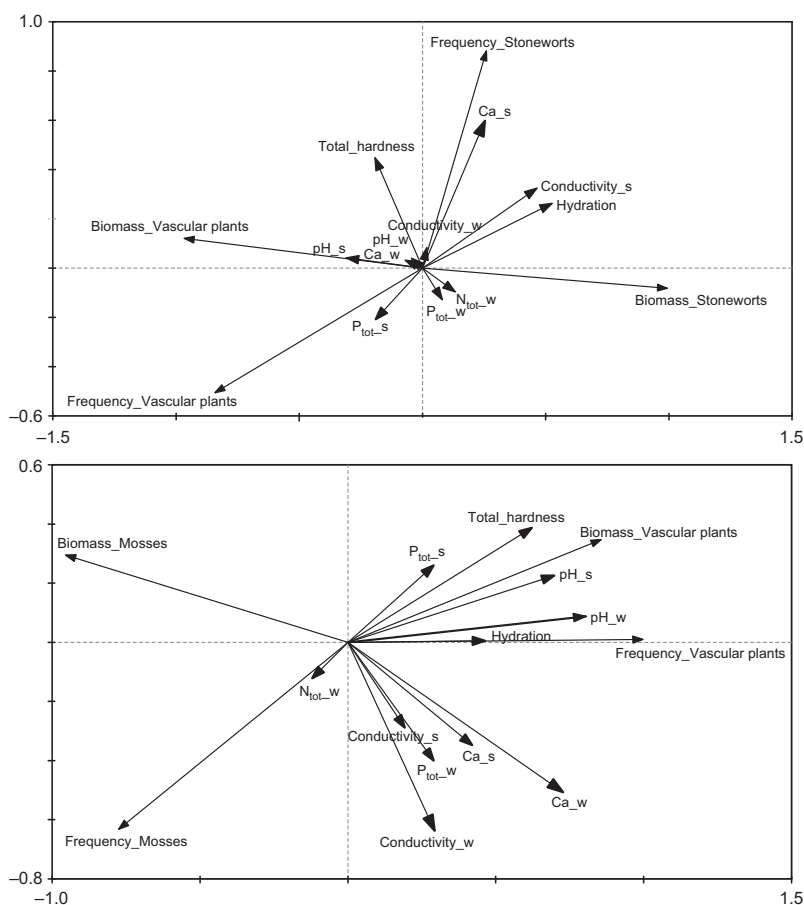
Table 3. Frequency (%) of submerged plants in samples taken from lakes (numbered 1–10) supplied with surface water (S) and groundwater (G).

Species	Frequency (lake no.)	
	S	G
Bryophytes		
<i>Drepanocladus aduncus</i>	–	3.7 (8, 9)
<i>Fontinalis antipyretica</i>	3.8 (2)	5.8 (6, 8)
<i>Sphagnum denticulatum</i>	67.7 (1, 2, 4, 5)	–
<i>Warnstorfia exannulata</i>	5.0 (1, 2, 4)	–
Vascular plants		
<i>Batrachium circinatum</i>	–	0.13 (6)
<i>Ceratophyllum demersum</i>	–	8.0 (6–9)
<i>Elodea canadensis</i>	–	7.7 (6–9)
<i>Isoetes lacustris</i>	26.5 (1, 2)	2.9 (10)
<i>Juncus bulbosus</i>	1.1 (1, 2)	–
<i>Lobelia dortmanna</i>	11.3 (1, 2)	1.1 (10)
<i>Myriophyllum spicatum</i>	–	16.0 (6, 8, 9)
<i>Polygonum amphibium</i>	0.3 (2)	1.0 (9)
<i>Potamogeton filiformis</i>	–	0.2 (6)
<i>Potamogeton gramineus</i>	–	1.2 (9)
<i>Potamogeton lucens</i>	–	1.7 (6)
<i>Potamogeton friesii</i>	–	1.1 (6)
<i>Potamogeton × nitens</i>	–	0.5 (9)
<i>Potamogeton pectinatus</i>	–	13.3 (6, 7, 9)
<i>Potamogeton perfoliatus</i>	–	4.9 (6, 9)
<i>Potamogeton praelongus</i>	–	8.9 (6)
<i>Stratiotes aloides</i>	–	0.6 (6, 9)
Stoneworts		
<i>Chara contraria</i>	–	4.1 (6–8)
<i>Chara delicatula</i>	–	9.5 (9, 10)
<i>Chara fragilis</i> (= <i>Ch. globularis</i>)	–	0.08 (9)
<i>Chara rudis</i>	–	0.2 (6, 7)
<i>Chara tomentosa</i>	–	11.5 (6–8)
<i>Nitella flexilis</i>	–	26.0 (6, 8, 9)
<i>Nitella syncarpa</i>	–	1.5 (2)
<i>Nitellopsis obtusa</i>	–	8.8 (6, 7, 9)

Table 4. Biomass and frequency of bryophytes, vascular plants and stoneworts in lakes supplied with surface water (S) and groundwater (G). DW = dry weight. Significant difference between lake groups (G, S) indicated as follows: * $p < 0.05$, ** $p < 0.001$.

	Mean \pm SD		Median	
	S	G	S	G
Biomass (g DW 0.1 m^{-2})				
Bryophytes	$9.6 \pm 6.2^{**}$	$1.6 \pm 2.1^{**}$	7.9	1.1
Vascular plants	$8.9 \pm 6.8^*$	$5.1 \pm 6.5^*$	6.6	3.2
Stoneworts	$2.8 \pm 3.4^*$	$13.8 \pm 20.5^*$	1.7	7.2
Frequency (%)				
Bryophytes	$72.5 \pm 35.1^{**}$	$8.4 \pm 12.4^{**}$	74.3	4.7
Vascular plants	$23.9 \pm 29.7^*$	$40.1 \pm 25.2^*$	15.6	35.0
Stoneworts	$3.9 \pm 12.1^{**}$	$59.7 \pm 23.2^{**}$	0.5	42.6

Fig. 3. RDA ordination of aquatic plant frequency and biomass in lakes supplied with surface water (top) and groundwater (bottom) vs. parameters characterizing water and sediment. Abbreviations: pH_w = pH of water, Conductivity_w = conductivity of water ($\mu\text{S cm}^{-1}$), Ca_w = concentration of calcium ions in water (mg l^{-1}), Total_hardness = total hardness of water (mg CaO l^{-1}), P_{tot-w} = concentration of total phosphorus in water (mg l^{-1}), N_{tot-w} = concentration of total nitrogen in water (mg l^{-1}); pH_s = pH of sediment, Conductivity_s = conductivity of sediment ($\mu\text{S cm}^{-1}$), Hydration = hydration of sediment (%), Ca_s = calcium content in sediment (mg g^{-1} DW), P_{tot-s} = concentration of total phosphorus in sediment (mg g^{-1} DW).



tistically significant relationship with the depth gradient ($p < 0.01$): the shallower the water, the larger the biomass of vascular plants and their share in total plant biomass. Vascular plant biomass depended to a small extent on sediment pH and the calcium concentration in the water (Fig. 3). Stoneworts had the highest biomass ($13.8 \pm 20.5 \text{ g DW } 0.1 \text{ m}^{-2}$); high standard deviation indicates that it was highly variable. Their biomass in the samples ranged widely from 0.1 to $118.7 \text{ g DW } 0.1 \text{ m}^{-2}$. An analysis of the distribution of mean stonewort biomass shows that the majority of these plants were found between 3 and 7 m (62.7% of total biomass). The biomass of stoneworts, like the frequency of their occurrence, was dependent on the physical and chemical properties of sediment, but also to some extent on water properties. The physicochemical properties of sediment explained 32.0% of biomass variation in this set of species ($r^2 = 0.32$, $p < 0.001$). In the relationship sediment–stonewort

biomass, conductivity was the most important (Fig. 3). RDA confirmed these relationships.

Mean bryophyte biomass and that vascular plants was much higher in the surface-fed lakes than in the lakes supplied with groundwater and (Table 4). In both lake types, biomass was controlled by similar factors such as sediment pH, total hardness and the calcium content in water. Stoneworts, dominating total plant biomass, occurred predominantly in lakes supplied with groundwater. Stonewort biomass was controlled above all by sediment conductivity.

Nutrient and non-nutrient factors

In both types of lakes frequency of species depended above all on the non-nutrient variables of the water (NNVW: $r^2 = 0.94$, $\chi^2 = 610.70$, $p < 0.000001$, $\text{df} = 124$; Fig. 4). The first (most significant) canonical element was connected with

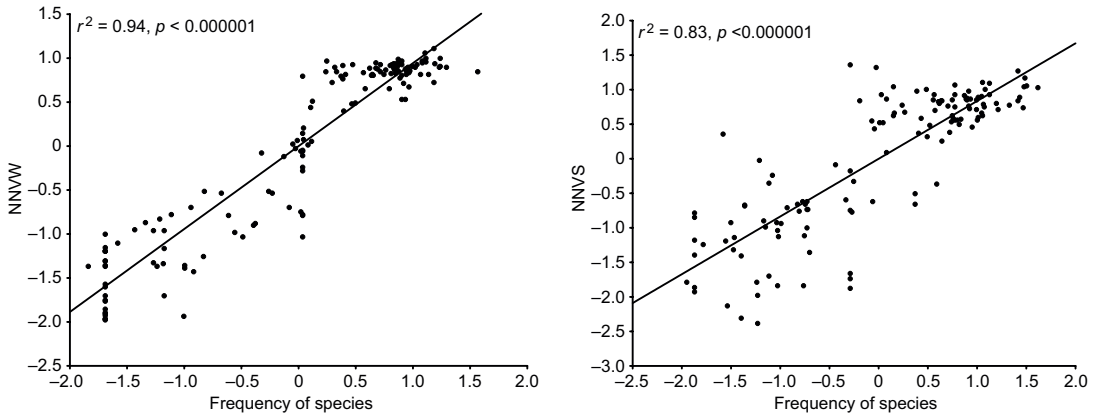


Fig. 4. Canonical correlation of frequency of species with non-nutrient variables of water (NNW, on the left) and with non-nutrient variables of sediment (NNVS, on the right).

water pH ($r^2 = 0.81$), and the second with conductivity ($r^2 = 0.42$). The correlation of species frequency with non-nutrient sediment variables (NNVS) was also high ($r^2 = 0.83$, $\chi^2 = 220.50$, $p < 0.000001$, $df = 93$). Species frequency did not correlate with nutrient sediment variables (NVS: $p = 0.15$, $df = 64$).

We noted some interesting relationships between water and sediment properties and the frequency of individual plant species. Multiple regression analysis indicated that *Nitellopsis obtusa* was weakly correlated with water and sediment conductivity ($r = 0.30$, $p < 0.0001$), *Chara rudis* with sediment conductivity ($r = 0.35$, $p < 0.001$), *Myriophyllum spicatum* with water pH ($r = 0.45$, $p < 0.001$), and *Sphagnum denticulatum* also with water pH ($r = -0.70$, $p < 0.001$).

We also analysed the correlations between the biomass of 29 species and the nutrient and non-nutrient variables of water and sediment in both types of lakes. In the surface-fed lakes, non-nutrient factors of both water and sediment affected plant biomass more strongly than nutrient variables did (Table 5). Plant biomass in the groundwater-fed lakes was affected even more by non-nutrient than by nutrient factors.

Generally, environmental variables were more strongly correlated with species frequency than with biomass. Regardless of the type of water supply, both the frequency and biomass of aquatic plants were much more strongly correlated with non-nutrient than with nutrient variables. The correlations with non-nutrient vari-

ables were strongest for bryophyte frequency in lakes supplied with surface water (Fig. 4). For stoneworts as well, frequency and biomass depended mainly on non-nutrient variables. Only the frequency of vascular plants was controlled to a small extent by nutrient variables.

Discussion

The environmental conditions of water and sediment differed between the outwash lakes fed with surface water and groundwater (Table 2 and Fig. 2). The lakes supplied with surface water

Table 5. Relationships between aquatic plant biomass (g DW 0.1 m⁻²; DW = dry weight) and non-nutrient and nutrient factors in lakes supplied with surface water and groundwater. NNW = non-nutrient water variables, NNVS = non-nutrient sediment variables, NVW = nutrient water variables, NVS = nutrient sediment variables. $p < 0.00001$ for all variables.

Variable	r^2 canonical	χ^2	df
Surface water			
NNW	0.60	168.7	24
NNVS	0.41	98.6	18
NVW	0.36	87.7	12
NVS	0.25	63.2	11
Groundwater			
NNW	0.56	440.6	104
NNVS	0.54	366.5	81
NVW	0.26	141.1	54
NVS	0.30	164.7	52

received nutrient-poor, acidic water together with allochthonous, mainly mineral, clastic material. The intensity of surface flow is a function of the catchment slope and the extent of forest cover. Allochthonous clastic material is deposited in limnic sediments, and it alters them in different ways (Birks and Birks 1980). The importance of supplied biogenic substances is stressed in the hydroecological literature (Punning *et al.* 2004). Minerogenic substances such as silica (SiO_2), which plays an important role in geochemical cycles, are mentioned less frequently (Tréguer and Pondaven 2000). Supply of allochthonous silica is of greater importance in shallow lakes fed with surface water. In groundwater-fed lakes the underground water is a source of various salts, especially calcium (Shapley *et al.* 2005, Myrbo and Shapley 2006), which, as we showed here, was one of the most significant factors affecting aquatic-plant frequency and biomass.

Our studies indicated that calcium concentration, conductivity and pH were the main factors controlling water properties (Table 2 and Fig. 2). Toivonen and Huttunen (1995), Nurminen (2003) and Kolada *et al.* (2005) also indicated the crucial role calcium in differentiation of lake environments. The lakes fed with surface water flowing over sandy catchment slopes were poor in calcium, acidic and nutrient-poor, while those supplied with groundwater were rich in calcium, alkaline, and nutrient-poor (Table 2).

In shallow acidic lakes supplied with water flowing over outwash catchment slopes, the shallow littoral zone is usually dominated by isoetids, and the deep littoral zone by mosses (Szmeja 1994b, Murphy 2002). In such lakes, low calcium concentration, pH and conductivity were the main factors controlling frequency and biomass of plants. The vegetation structure is simple. Concentrations of mosses, especially aggregations of *Sphagnum denticulatum*, occupy largest parts of the bottom in such lakes (Gos and Banaś 1999, Banaś 2002, Szmeja 2010). The dominance of this species increases with decreasing pH and with decreasing intensity of the main controlling factor, that is, the concentration of calcium and its derivatives (Fig. 3). This plant is also a common component of acidic lakes outside outwash plains (Ilyashuk 1999, 2002, Gunnarsson *et al.* 2004).

The vegetation structure was more complex in the lakes supplied with calcium-rich groundwater than in the shallow ones fed mainly with surface water. Many species occurred there, predominantly *Charales*, *Potamogeton* sp. div. and *Cormophyta*, and consequently species diversity was higher than in the other lake group. Mosses as a vegetation component were negligible.

In both types of lakes, species composition of aquatic plants and biomass in the littoral zone were connected with pH, calcium and with the form of available inorganic carbon used in photosynthesis. In lakes, pH regulates inorganic carbon forms (Maberly and Spence 1983). Heegaard *et al.* (2001) and Nurminen (2003) emphasized the crucial role of pH and hence the form of inorganic carbon. Maberly and Spence (1983) and Madsen and Sand-Jensen (1991) found that in lakes supplied with surface water, mosses and isoetids, which mainly use free CO_2 , were the dominant plants. According to Vestergaard and Sand-Jensen (2000), the species composition is negatively correlated with pH ($r = -0.80$) and alkalinity ($r = -0.91$). However, a study conducted in Finnish lakes showed that the number of macrophyte species and pH were positively correlated ($r = 0.639$, $p < 0.01$; Nykänen *et al.* 2005). In peatland lakes, frequency of mosses is related to calcium concentration ($r = -0.52$; Banaś *et al.* 2012). Stoneworts and vascular plants dominating in groundwater-fed lakes mainly use HCO_3^- . For example, Lodge *et al.* (1989) found significant rank correlation of vascular plants and stoneworts biomass with groundwater velocity (Sperman's rank correlation: $r_s = 0.46$, $p < 0.01$) in a lake supplied with groundwater, rich in calcium and HCO_3^- .

Physical and chemical factors controlling the structure of submerged plants are largely consequences of primary processes responsible for the formation of lake basins and their catchments. The type of geological deposit and topography of catchments are good criteria for the classification of environments in lakes (Kolada *et al.* 2005). The basis for this claim is that the calcium concentration in the water of lakes depends mainly on the type of geological deposit. According to Heegaard *et al.* (2001), non-nutrient variables, e.g. calcium concentration and water conductivity correlated ($r = 0.62$ and $r = 0.48$,

respectively) with bedrock acidity level (acidic, mildly basic and limestone). Studies of 848 boreal catchments showed that geomorphology and land use explain 26.7% of the variability in emergent aquatic macrophyte occurrence and 21.2% of the variability in emergent aquatic macrophyte percentage cover (Alahuhta *et al.* 2011). In outwash areas, the impact of catchment on environmental conditions, frequency and macrophyte biomass is high in small and shallow lakes with surface supply. In lakes dominated by stoneworts and vascular plants environmental factors of catchment are compensated by the supply of groundwater.

For both types of water supply, the frequency and biomass of submerged plants were controlled more strongly by non-nutrient than by nutrient factors (Table 4 and Fig. 2). In the surface-fed lakes, the frequency of mosses and vascular plants was controlled mainly by pH. This result finds confirmation in studies of other lakes with comparable acidity and surface water supply (Ilyashuk 1999, Bociąg 2003, Szmeja 2010). The correlation of the frequency of 29 aquatic plant species with non-nutrient factors was high ($r^2 = 0.94$, $\chi^2 = 610.70$, $p < 0.000001$). The same was true for the biomass of those 29 species. Szmeja (1994b) and Bociąg and Szmeja (2001) reported similar relationships between non-nutrient factors (mainly pH and conductivity) and plant frequency and biomass. The important role of pH and calcium in the variation of macrophyte biomass and composition was pointed out by KISSOON *et al.* (2013), where the seven analysed factors controlling pH explain the highest percentage of variation of macrophyte biomass.

In the outwash lakes located in acidic, sandy and barren formations, the role of non-nutrient variables as environmental factors controlling frequency and biomass was much more important than that of nutrient factors. The type of water supply affected environmental conditions in the lake water and sediment, as well as the biomass of aquatic plants. Vegetation structure expressed as the number, frequency and biomass of species was simple in the lakes with surface water supply, and complex in the lakes with groundwater supply. Such a basic difference is of fundamental significance for the study of environmental factors controlling frequency and

biomass of aquatic plants, and for the protection of lake biodiversity.

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